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The larval shells of *Graptacme agilis*, *Entalina tetragona* and *Pulsellum lofotense* (Scaphopoda) from the Mediterranean

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KEY WORDS: Scaphopoda, *Graptacme*, *Entalina*, *Pulsellum*, Larval shells, Pleistocene, Recent, Mediterranean.

RIASSUNTO Sono state esaminate le conchiglie larvali degli scafopodi *Graptacme agilis* (Sars M. in Sars G.O., 1872), *Entalina tetragona* (Brocchi, 1814) e *Pulsellum lofotense* (Sars M., 1865), su materiale mediterraneo (pleistocenico ed attuale per le prime due specie). Sono stati riconosciuti due tipi morfologici, ovvero una conchiglia larvale "lunga" in *G. agilis* ed una "breve" in *E. tetragona* e *P. lofotense*, in accordo con quanto noto in letteratura. Il termine *praetubulus* è proposto per la conchiglia larvale degli scafopodi.

ABSTRACT The larval shells of the scaphopods *Graptacme agilis* (Sars M. in Sars G.O., 1872), *Entalina tetragona* (Brocchi, 1814) and *Pulsellum lofotense* (Sars M., 1865) are examined on Mediterranean material (Pleistocene and Recent for the first two species). Two morphological types are recognized, *i.e.* a "long" larval shell in *G. agilis* and a "short" one in *E. tetragona* and *P. lofotense*, in accordance with which is known in literature. The term *praetubulus* is proposed for the scaphopod larval shell.

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INTRODUCTION

Whereas the gastropod and the bivalve larval shells are currently examined and successfully used in systematic and evolutionary studies, the early developmental stages of scaphopods are still poorly known. This is mainly due to the rareness of these early stages. Since the apical portion of the scaphopod shell becomes resorbed during the post-larval growth, the larval stages can be only preserved in very young, small and not easily collectable specimens, which may be also hard to be identified at species level.

The knowledge of the larval scaphopod shells was greatly improved by two recent works, ENGESER *et al.* (1993) and STEINER (1995), where the general morphological and morphometric features were first pointed out, a descriptive terminology proposed, and at least two morphological types recognized.

In the present work, the larval shells of three deep-sea species from the Mediterranean are dealt with, *i.e. Graptacme agilis* (M. Sars in G.O. Sars, 1872), *Entalina tetragona* (Brocchi, 1814) and *Pulsellum lofotense* (M. Sars, 1865). Pleistocene and Recent material was examined for the first two species. The larval shells of *E. tetragona* [as *E. quinquangularis* (Forbes, 1844)] and *P. lofotense* from the North Atlantic (Norway) were previously treated by STEINER (1995). He also reported the larval shell of *Antalis occidentalis* Stimpson, 1851 (probably misidentified, see discussion).

Materials and methods

The examined material consists of very young (post-larval) shells, sorted from 500-200 µm sieved fractions.

Thirteen young shells of *E. tetragona* were obtained from two Pleistocene sites, namely Furnari (northeast Sicily, Tyrrhenian side) and Bianco (southern Calabria, Ionian side). The molluscan assemblages from both sites were treated by DI GERONIMO & LA PERNA (1997), who inferred palaeodepths >500 to 1,000 m. In these deposits *E. tetragona* and *G. agilis* are common species, together with *Cadulus ovulum* (Philippi, 1844) and *Gadila jeffreysi* (Monterosato, 1875). Seven young shells were also obtained from some box-corer stations off the Aeolian Archipelago, Southern Tyrrhenian Sea (EOCUMM94 and EOCUMM95 Cruises), in 300-1,219 m.

Two young shells of *G. agilis* were obtained from two EOCUMM95 stations (786 and 1,521 m), and twenty-one from the same Pleistocene sites as for *E. tetragona*.

Three young shells of *P. lofotense* come from an EOCUMM94 station in 300 m.

Shell measurements refer to the whole length (L) and to the maximum diametre (D) of the larval shell (= L-pc and D-pc of STEINER, 1995, fig. 2). They were taken by means of an eyepiece micrometre.

Systematic remarks

According to the most recent classification of Scaphopoda (STEINER, 1991, 1992; SCARABINO, 1995), three families are represented by the studied species, *i.e.* Dentaliidae Da Costa, 1776 (*G. agilis*), Entalinidae Chistikov, 1979 (*E. tetragona*) and Pulsellidae Scarabino in Boss, 1982 (*P. lofotense*). The first family belongs to the order Dentaliida Da Costa, 1776, the others to Gadilida Starobogatov, 1974.

G. agilis has been hitherto reported as *Dentalium* or *Antalis agile* (e.g. CAPROTTI, 1979, SABELLI *et al.*, 1990), but neither *Dentalium* nor *Antalis* represent a good systematic allocation for this species, which must be referred to *Graptacme* Pilsbry & Sharp, 1897 (type-species *Dentalium eboreum* Conrad, 1846, West Atlantic). *Graptacme* is characterized by a slender and faintly arcuate shell. Fine and close riblets occur on the apical portion, leaving the anterior half polished. The cross section is rounded both posteriorly and anteriorly.

E. tetragona is the type species of *Entalina* Monterosato, 1872. The Recent (from the Aegean Sea) *Dentalium quinquangulare* Forbes, 1844 is often synonymized with the fossil (from the North Italy Pliocene) *D. tetragonum* Brocchi, 1814 and actually no definitive evidence of two distinct species has been ever reported. Sculpture is raher variable and the Pleistocene shells are often smoother than Recent ones. The "smooth" Early Pleistocene form described as *Entalina expolita* by DELLA BELLA & TABANELLI (1996) should be synonymized with *E. tetragona*.

P. lofotense is the type-species of *Pulsellum* Stoliczka, 1868.

Terminology

ENGESER *et al.* (1993) recognized and termed the main morphological features of a typical scaphopod (dentaliid) larval shell ("protoconch"). When fully developed, it shows a posterior bulging part with an apical opening, which is sometimes surrounded by a short pipe ("fumarium"). A "suture" ventrally joins the "genae", *i.e.* the cheeck-like sides of the bulging part. The anterior region is cylindrical and bears one to some "annulations". A "constriction" sometimes is also present.

STEINER (1995) agreed on this terminology, but ditinguished the larval shell into two stages, according to their ontogenetic appearance, *i.e.* the bulging posterior part as "protoconch A", and the fumarium and the anterior region as "protoconch B". He also focused the post-larval development, in which he distinguished an early stage ("teleoconch A") and a late one ("teleoconch B"), the latter marked by the adult sculpture onset.

Due to its peculiar morphology and ontogeny (see reviews by ENGESER *et al.*, 1995 and STEINER, 1996), the scaphopod larval shell is hard to be fully homologized with the gastropod protoconch or the bivalve prodissoconch. A specific term should be then introduced, and *praetubulus* (from the Latin *prae*=before and *tubulus*=small tube) is herein proposed.

RESULTS

The *praetubulus* of *G. agilis* (Figs. 1-5) is relatively thick, elongate, slightly dorsally inclined (Fig. 3), anteriorly annulated and apically extending in a well-developed fumarium. The genae are slightly inflated and the suture well-impressed. The fumarium is ventrally inclined (Figs. 3, 5), ca. 100 µm long in early post-larval shells, becoming shorter and ventrally notched in the older ones. Five to seven annulations are present, the lowermost ones being more prominent. Along the suture, the annulations become apically arched. The *praetubulus* length is 540-610 µm, the diametre ca. 200 µm. At the anterior ending, the shell wall is ca. 45 µm thick. The strength of annulations appears notably variabile in the Pleistocene material (the Recent one was too scarce to detect any variation), as well as the slenderness (see Figs. 3, 4, 5). The adult axial riblets become evident when the shell is ca. 1.5 mm long.

The *praetubulus* of *E. tetragona* (Figs. 8, 9) is bulb-shaped, smooth and glossy, with a somewhat sharp apical ending. A marked constriction and a single annulation are anteriorly present. The anterior ending is cylindrical, with concentric growth lines and dentritic ridges (Fig. 10). The genae are indistinct, the suture poorly developed, being probably fast "eaten" away by the ventral-ward extending apical opening. The length is ca. 360 µm, and the diametre 140-170 µm. Post-larval shells (up to 1.5 mm in length) resemble *Pulsellum* and show a well-preserved *praetubulus*, with a small apical opening. In larger shells (up to 2.5 mm), when the oral cross-section attains the typical pentagonal shape, the apical opening cuts the whole apical ending. A strongly reduced larval portion may rarely occur in larger shells. No remarkable difference was recorded between the Pleistocene and the Recent material.

P. lofotense also has a bulb-shaped, smooth and glossy *praetubulus* (Fig. 6), resembling that of *E. tetragona*, from which it differs mainly by having a more obtuse apical ending and less defined anterior constriction and annulation. The suture is short, wrinkled and the genae indistinct (Fig. 7). Short and ill-defined axial riblets occur on the anterior ending. The length is ca. 270 µm and the diametre ca. 100 µm.

Discussion

The larval shell reported from the North Atlantic as *Antalis occidentalis* by STEINER (1995) is really of *G. agilis*, as suspected by STEINER himself (pers. comm.), as no remarkable difference appears between the present material and the North Atlantic one, except for some size discrepancies. Actually, only size differences appear between the Mediterranean larval shells and the North Atlantic ones, the latter being smaller (from STEINER, 1995, tab. 2: L=465±69 µm, D=178±8 µm for "*A. occidentalis*"; L=264±31 µm, D=108±4 µm for *E. tetragona*; L=205±29 µm, D=109±4 µm for *P. lofotense*). The size differences seem to affect mainly the *praetubulus* length. It is worth noting that length measurements resulted as the most variable ones in the morphometric analysis performed by STEINER (1995).

ENGESER *et al.* (1993) pointed out two morphological types among the larval shells of scaphopods: a "short" one (200-290 µm), more or less bulbous and constricted near the anterior end, and a "long" one (360-800 µm), with the anterior part more or less annulated. A similar distinction was also recognized by STEINER (1995), who termed "type 1" the long larval shells (with well-defined protoconch A and B), and "type 2" the short ones, in which the bulging protoconch A is weakly distinguished. *E. tetragona* and *P. lofotense* have a short (type 2) *praetubulus*, whereas a long one (type 1) occurs in *G. agilis*. The hitherto overlooked axial or dendritic microsculpture on the ending portion, seems a frequent feature among the short *praetubuli*, being known in *E. tetragona*, *P. lofotense* and in the Indo-Pacific *Spadentalina ingrata* Scarabino, 1995 (SCARABINO, 1995, fig. 111b).

As reviewed by STEINER (1995), the long type occurs only in Dentaliida, while the short one occurs only in Gadilida. It should be anyway noted that the two undetermined fossil species of "*Entalinopsis*" reported by ENGESER *et al.* (1993), both showing short *praetubuli*, shoud be instead referred to the dentaliid genus *Paradentalium* Cotton & Godfrey, 1933, owing to their hexagonal apical cross-section (see SCARABINO, 1995: p. 216, but see also comments by ENGESER *et al.*, 1993: p. 88). If this systematic allocation proves to be correct, short *praetubuli* then may also occur in Dentaliida.

Figures 1, 2 - *Graptacme agilis*. EOCUMM95/15, 1,521 m (Southern Tyrrhenian Sea); ventral (1) and apical (2) views. Shell length 3.0 µm. Scale bars=100 µm. Figures 3, 4, 5 - *Graptacme agilis*. Bianco (Southern Italy, Pleistocene); lateral (3), latero-ventral (4) and latero-dorsal (5) views. Shell length 3.3 µm (3), 1.2 µm (4), 1.7 µm (5). The dorsal groove in fig. 5 is a scratch. Scale bars=100 µm. Figures 6, 7 - *Pulsellum lofotense*. EOCUMM94/18, 300 m (Southern Tyrrhenian Sea); lateral view (6) and detail of the suture (7). Shell length 1.3 µm (6) and 1.4 µm (7). Scale bars=50 µm. Figures 8, 9 - *Entalina tetragona*. Furnari (8) and Bianco (9) (Southern Italy, Pleistocene), lateral views. Shell length 1.3 µm (8), 1.2 µm (9). Scale bars=50 µm. Figure 10 - *Entalina tetragona*. EOCUMM95/7, 1,197 (Southern Tyrrhenian Sea); oblique ventral view of the anterior ending. Shell length 2.9 µm. Scale bar=50 µm.

STEINER (1995) stressed the lacking of larval material for *Cadulus subfusiformis* (Sars M., 1895), for which he found only early post-larval stages. Actually, only one species of Gadilomorpha is known as larval stage, *i.e.* the Paleocene *Gadila turgida* (Meyer, 1886) (ENGESER *et al.*, 1993). It is also worth noting the lacking of larval material of *Cadulus ovulum* and *Gadila jeffreysi* in the Pleistocene deep-sea sediments in which the *praetubuli* of *G. agilis* and *E. tetragona* were found, although in the same sediments, as well in other similar deposits (LA PERNA, 1994; DI GERONIMO *et al.*, 1998), both *C. ovulum* and *G. jeffreysi* are frequent. One of the hypothesis suggested by STEINER (1995), *i.e.* that the larval shell may be uncalcified in some Gadilomorpha, seems the most agreeable. STEINER also observed that the larval shell of *G. turgida* differs from all the others in being bell-shaped rather than bulbous, and assumed a similar shape for the *C. subfusiformis* larval shell. It should be finally noted that the current allocation of this last species, as well as of other allied species, in *Cadulus* Philippi, 1844 is unsatisfactory (DI GERONIMO & LA PERNA, 1997). It would fit better, but not fully, in the genus *Gadila* Gray, 1847.

ENGESER *et al.* (1993), suggested that the long and short larval shells are due to different types of development, *i.e.* to a long-living larval stage and to a short one respectively, but no data are available to support this hypothesis, as remarked by STEINER (1995). The two morphological types should be anyway regarded as related to unknown differences in the reproductive and developmental modalities of Dentaliida and Gadilida (*e.g.* as known for the modality of gamete releasing: STEINER, 1993). In this respect, it is worth noting that the *praetubulus* margin, i.e. the metamorphic line, appears chipped in the "thick-walled" *praetubulus* of *G. agilis* (see Figs. 1, 3), whereas it is clear-cut in the *E. tetragona* and *P. lofotense*, although their larval shells are thinner. This may suggest different modalities of transition to the post-larval stage, such as a developmental stasis (as benthic stage) once the *praetubulus* of *Graptacme* is fully developed and mineralized (as reviewed by STEINER, 1995, calcification is believed to occurs before or at metamorphosis).

The present difficulty in identifying the scaphopod larval shell at species level also needs to be stressed. The early stages by themselves may be hard to be correctly identified, due to the scarcity of morphological and diagnostical landmarks. Two cases are instructive in this respect: that of *Antalis occidentalis* by STEINER (1995) and that by RUGGIERI (1987), whose fossil larval shells of "*Dentalium rectum*" most probably pertain to two distinct dentaliids (see ENGESER *et al.*, 1993: p. 97).

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